

Behavioral Modes Arise From a Random Process in the Nudibranch *Melibe*

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Abstract. Stochastic analysis was applied to observations of spontaneous behavior in the carnivorous mollusc *Melibe leonina*. Six behaviors were defined that could be easily recognized on inspection and it was found that transitions between each of these behaviors could be fully described by a first-order random process without memory of past behavioral choices. The behaviors are organized by frequency of transition into two modes, a feeding mode and a resting mode. Transitions within modes are more likely than transitions between modes, and the feeding and resting modes are linked by a preferred pair of behavioral transitions. The amount of time spent in the feeding mode is positively correlated with body size, but the average length of a feeding episode is independent of size. This suggests that body size regulates the probability of entry into feeding behavior but does not influence the basic pattern of feeding. In the presence of food the animals express nearly continuous feeding behavior, suggesting that food reduces the probability of exiting the feeding mode. This model of spontaneous behavior in *Melibe* is used to form hypotheses amenable to further exploration through neurophysiological experiments.

Introduction

Analysis of animal behavior provides the background necessary for studies of the underlying neural circuitry and circuit function. Such analysis sometimes permits

useful predictions to be made about specific properties of the underlying neural networks—for example, the extent to which stochastic processes in the nervous system influence the ordering of behaviors in a sequence (Heiligenberg, 1973). Molluscs have been used to advantage by neuroethologists because the relatively limited behavioral repertoires and accessible nervous systems of these animals permit investigation of synaptic connections between identified neurons (Davis *et al.*, 1974; Kandel, 1976; Gelperin, 1983; Willows, 1985; Getting, 1989). Most studies have concentrated on reflex or conditioned responses evoked by stimuli presented in defined patterns, an approach that simplifies the design of electrophysiological experiments. Important generalizations about the organization of small neural networks have emerged from such studies, including the idea that animal behaviors are organized in hierarchies of successively more dominant or more strongly commanded responses (Tinbergen, 1951; Davis *et al.*, 1977; Getting, 1989).

Concentration on evoked and conditioned behavior ignores, however, the phenomenon of unstimulated behavioral choice (Lorenz, 1981). We recorded the temporal sequence of behaviors in the nudibranch *Melibe leonina* as it evolved spontaneously in the absence of overt stimulation, then used standard techniques of random-process analysis to model this behavioral sequence (Chatfield and Lemon, 1970). Our results lead to several conclusions. (1) In the absence of overt stimuli, the choice of behavior is well described by a first-order random process. (2) Consideration of the transition probabilities of this process indicates that spontaneous behaviors in *Melibe* fall into two behavioral modes. (3) There is a preferred transition that links the behavioral modes. (4) The presence of strong stimuli such as food organisms influences the individual transition probabilities. Fi-

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nally, (5) physiological parameters, such as body size, also influence behavioral transition probabilities.

Melibe is well suited to this study. We were able to define a set of six canonical behaviors that are easily recognized on inspection. Transitions between these behaviors were infrequent and could be adequately scored by making observations at 15-min intervals. This permitted us to examine behavioral transitions over an extended time period and to perform replicate sets of observations. Furthermore, the *Melibe* central nervous system is suitable for microelectrode and optical recording methods for monitoring cellular activity in identified neurons in restrained whole animal preparations (Willows, 1973; Cohen *et al.*, 1991). This provides the opportunity to study mechanisms of spontaneous behavioral expression at the level of neural networks.

Materials and Methods

Melibe leonina, a carnivorous nudibranch of the family Tethyidae, is distinguished by an extended oral veil used in prey capture (Agersborg, 1923). Two groups of 10 animals were studied between 1 and 29 May. Adult specimens weighing 40–250 g were collected from the *Macrocystis* kelp forest in Monterey Bay, California. The animals were held in 45-liter tanks supplied with continuously flowing sand-filtered seawater for 2–28 days before observations were begun. Changes in motivation were minimized by allowing the animals to acclimate to the experimental tanks and by simulating a natural environment. No correlation was found between the number of days in captivity and the behavioral pattern. For observation, animals were placed in five identical 17-liter acrylic plastic tanks provided with flowing sand-filtered seawater and a frond of kelp. The tanks rested on sea tables in a roofed aquarium building where they were protected from direct sun and rain but exposed to natural cycles of light and temperature. Methylene blue dye was injected into the first right ceratum of one animal of the two animals in each tank to facilitate identification. The animals were fed every other day at the same time with the same amount of their natural food, live mysid shrimp collected from the wild. The animals were otherwise left undisturbed for eight days of observation, which included four nonfeeding days from each group.

We define six behaviors that occur frequently but without overlap in the absence of overt stimulation (Fig. 1). Together they account for greater than 90% of the activity in the observation tanks. The behaviors are distinguished by characteristic body postures involving the oral hood, the rhinophore processes, and the cerata, as well as by the presence or absence of pedal locomotion. The six behaviors are as follows: (1) Feeding (F): rhythmic extension and contraction of the oral hood in a cast-

ing motion through the water (Hurst 1968; Watson and Trimarchi, 1992). (2) Open hood (OH): full extension of the oral hood with the cerata and rhinophore processes extended. (3) "Alert"/processes extended posture (AL): oral hood partially closed with the oral tentacles tucked inside, cerata and rhinophore processes extended. (4) Roaming/open hood (R/OH): OH behavior combined with pedal locomotion. (5) Roaming/processes extended (R/AL): AL behavior combined with pedal locomotion. (6) Resting (RST): locomotion absent, hood closed and held against the substrate, cerata contracted against the sides of the body, rhinophore processes folded down.

Several other behaviors occurred too infrequently for analysis. These included (1) pedal locomotion in the RST posture; (2) the "crumple" reflex, an alarm response elicited by tactile or vibratory stimuli and characterized by forceful contraction of most of the body wall musculature (Scott, 1990); (3) swimming; (4) egg-laying. Copulation was observed occasionally but was not scored independently because the six behaviors we followed occurred at the same frequency independent of copulation.

Observations were made at 15-min intervals for 6 hours a day beginning between 0800 and 1200 h. During preliminary studies, we observed behavior continuously for periods of several hours. By parsing the data into time periods of varying duration, we determined that a 15-min sample interval is adequate to capture behavioral transitions. Observations from one nonfeeding day for the 10 animals in group 1 are tabulated in Figure 2. It is apparent that behavior changes infrequently and that individuals tend to perform the same behavior over several time points. On feeding days the animals spent about 80% of their time performing feeding behavior (F), indicating that the presence of prey organisms has a powerful influence on behavioral choice (Watson and Trimarchi, 1992; Watson and Chester, 1993). Analysis was limited to nonfeeding days in order to include a more diverse range of behaviors and to obtain observations under relatively constant physiological conditions.

Results

The frequency of occurrence of each of the 36 possible behavioral transitions, including consecutive occurrences of the same behavior, was tallied by observing behavior at 15-min intervals. The data are expressed in Table 1 as transition probabilities for each of two replicate, 4-day experiments. The sum of the transition probabilities from a given starting behavior is normalized to 1.0. The predominance of certain one-step transition probabilities over others suggests that the six behaviors can be grouped into two distinct behavior modes (Fig. 3). Behaviors F, OH, and R/OH form the feeding mode, while

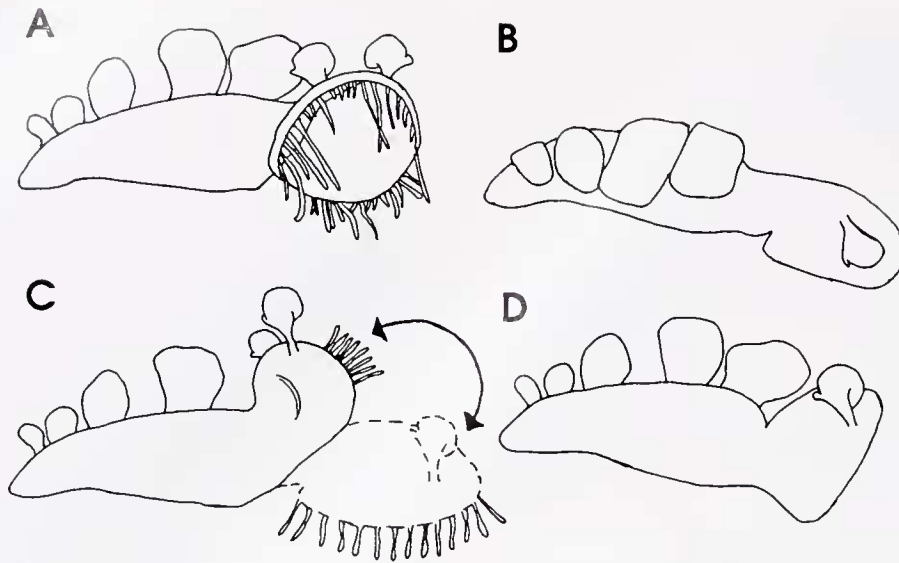


Figure 1. Body postures during six behaviors: (A) Open hood (OH) and roaming/open hood (R/OH) behaviors. (B) Resting (RST) behavior. (C) Feeding (F) behavior. (D) "Alert"/processes extended (AL) and roaming/alert (R/AL) behaviors.

behaviors RST, AL, and R/AL form the resting mode. This grouping of behaviors is based on the observation that transitions among mode elements occur much more frequently than transitions to behaviors outside of the mode. The frequencies of intermode transitions are listed in Table II. This qualitative observation is borne out by calculating between-mode transition frequencies for all possible ways of grouping the six behaviors into two modes. The correct mode structure will give fewer between-mode transitions than any other grouping.

There are 25 ways to structure two modes: 10 in which each mode contains three behaviors, and 15 in which one

mode contains two behaviors and the other contains four. For data set 1, the number of between-mode transitions for the mode structure proposed in Figure 3 was 145, whereas between-mode transitions for the other possible groupings ranged from 267 to 389. This supports the behavioral relationships diagrammed in Figure 3. According to this analysis, animals stay in one mode for an average of 1 hour and 11 minutes (5.2 observation intervals) before switching to the other.

Transitions between modes occur most frequently between behaviors OH and AL in either direction. The OH to AL transition accounts for 35% of all transitions from

THURSDAY, MAY 9, 1991, 0900-1500 hrs

interval #

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1A	R/OH	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
4B	OH	OH	F	F	OH	R/OH	F	OH	OH	AL	OH	OH	F	F	OH	OH	OH	OH	OH	AL	OH	OH	OH	F	
2A	R/OH	F	AL	R/AL	RST	AL	R/AL	RST	RST	R/OH	AL	OH	AL	OH	OH	OH	R/OH	RST	OH	R/AL	RST	RST	RST	RST	R/OH
2B	RST	R/OH	OH	R/AL	AL	AL	R/AL	AL	CR	RST	RST	R/AL	RST	RST	RST	R/AL	CR	AL	RST	RST	AL	RST	RST	RST	R/AL
3A	RST	OH	R/AL	OH	OH	OH	OH	OH	OH	OH	OH	OH	OH	OH	OH	OH	RST	OH	R/OH	OH	OH	R/OH	F	OH	F
3B	RST	RST	RST	RST	AL	AL	R/AL	AL	AL	AL	AL	AL	AL	AL	AL	R/AL	R/AL	AL	R/AL	AL	AL	R/AL	R/AL	R/OH	R/AL
4A	R/OH	RST	OH	RST	R/OH	OH	OH	OH	OH	OH	OH	OH	AL	OH	OH	AL	AL	AL	OH	AL	AL	S	AL	OH	OH
1B	RST	RST	RST	RST	RST	RST	RST	RST	RST	RST	RST	RST	RST	RST	RST	RST	RST	RST	RST	AL	RST	RST	RST	RST	RST
5A	F	F	R/OH	R/OH	RST	R/AL	RST	R/AL	OH	OH	R/OH	RST	R/OH	AL	R/OH	R/AL	OH	R/OH	R/AL	AL	RST	RST	OH	R/OH	RST
5B	RST	RST	RST	AL	AL	AL	AL	AL	AL	AL	AL	AL	AL	AL	AL	AL	R/AL	AL	R/AL	RST	AL	AL	R/AL	R/AL	RST

Figure 2. Sample data set from one full day of observations. Observations of each of 10 animals were made at 15-min intervals for 6 h. The duration of a behavior in continuous intervals is referred to as its dwell time. An example of a seven-interval dwell time in the open hood (OH) behavior can be seen in animal 4A from intervals six to twelve. Abbreviations: Feeding (F), open hood (OH), "Alert"/processes extended posture (AL), roaming/open hood (R/OH), roaming/processes extended (R/AL), resting (RST), crumple (CR), and swimming (S).

Table I

Transition probabilities between all behaviors for both sets of data

SET 1		Ending behavior					
Starting behavior	F	OH	R/OH	AL	R/AL	RST	
F	0.597	0.223	0.095	0.038	0.019	0.028	
OH	0.183	0.486	0.115	0.101	0.014	0.101	
R/OH	0.299	0.253	0.218	0.080	0.151	0.226	
AL	0.041	0.142	0.027	0.473	0.122	0.196	
R/AL	0.085	0.149	0.085	0.298	0.149	0.234	
RST	0.040	0.081	0.054	0.117	0.054	0.664	

SET 2		Ending behavior					
Starting behavior	F	OH	R/OH	AL	R/AL	RST	
F	0.459	0.208	0.138	0.101	0.075	0.019	
OH	0.188	0.370	0.087	0.268	0.043	0.043	
R/OH	0.293	0.200	0.227	0.093	0.120	0.067	
AL	0.065	0.094	0.039	0.526	0.101	0.175	
R/AL	0.135	0.122	0.135	0.446	0.122	0.041	
RST	0.005	0.020	0.010	0.256	0.054	0.655	

Each row of probabilities totals 1.00. Probabilities for transitions occurring within a behavioral mode are given in boldface.

the feeding to the resting mode, and the AL to OH transition accounts for 30% of transitions from the resting to the feeding mode. None of the 16 other possible between-mode transitions accounted for more than 15% of the transitions in either direction.

Individual variability

The time spent in each behavior varied a great deal between individual animals. As a measure of this vari-

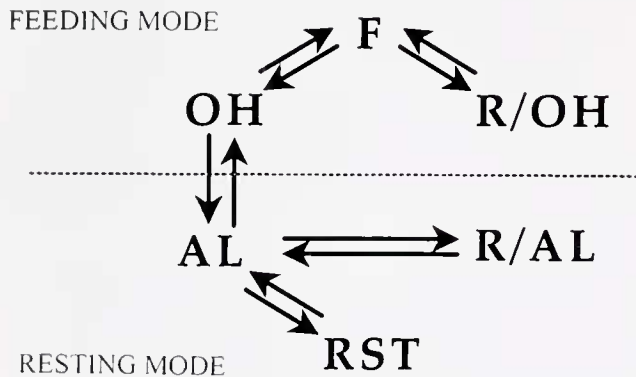


Figure 3. Feeding and resting modes. Arrows indicate the 10 most frequent transitions between different states. The mode structure minimizes intermode transitions; all other possible mode arrangements were considered (see text).

Table II

Transition probabilities within and between modes

Starting from:	Probability that the next transition is to:	
	Feeding mode	Resting mode
Feeding mode	0.79	0.21
Resting mode	0.18	0.82

ability, we calculated coefficients of variation (CV) for the number of transitions from a behavior back to itself (*i.e.*, $F \rightarrow F$) using the second set of 10 animals. The CV ranged from 64% to 157%. Some of the variability can be linked to a physiological correlate. For example, we found that body weight and time spent in the feeding mode are positively correlated ($r = 0.87$; Fig. 4). An 80-g individual spent 10% of the time in the feeding mode as compared to 80% for a 250-g animal. A similar correlation exists between size and time spent in the feeding (F) behavior within the feeding mode. The 250-g animal spent 58% of the total time in F, but the 80-g animal did not exhibit this behavior at all. This bias on both inter- and intramodal transition probabilities may reflect a difference in the nutritional needs of small *vs.* large animals and is worthy of further study. We did not find a correlation between body size and average dwell time in the F behavior in the absence of food organisms. This suggests that large animals enter feeding behavior more often than small ones, but that the duration of feeding episodes is about the same once feeding begins. Although body size has little effect on feeding dwell time, this pa-

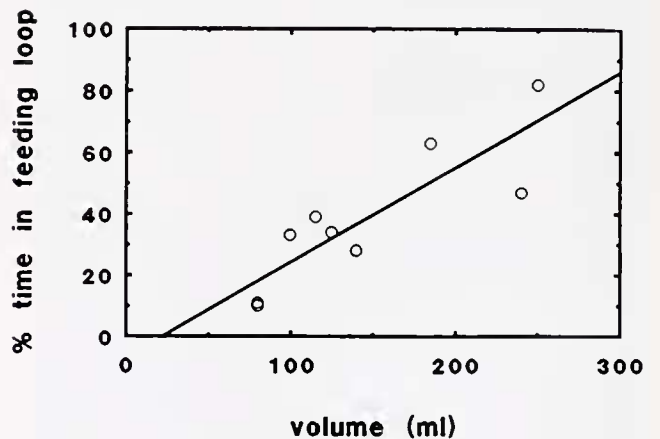


Figure 4. Body size and total time spent in the feeding mode are correlated. Data taken from set 2. Total time in the feeding mode from Figure 3 was calculated by counting the total number of intervals spent in feeding mode behaviors. Body volume was determined by water displacement. The correlation coefficient is $r = 0.87$.

parameter is influenced by the presence of food; Watson and Trimarchi (1993) have shown that dwell time varies inversely with the concentration of available prey.

Two-step transition probabilities

A sequence of behavioral acts is stochastic if the transition from one behavior to the next is independent of preceding behavioral changes. If this is so, the frequency of two-step transitions observed experimentally should match the transition frequencies predicted from a two-step stochastic model. Expected probabilities for two-step transitions were calculated from the measured one-step probabilities following the equation $P(a \rightarrow b \rightarrow c) = P(a \rightarrow b) * P(b \rightarrow c)$, where a, b, and c represent any of the six canonical behaviors. Behavioral observations from the 10 individuals in each data set were pooled and used to tabulate the probability of occurrence of each of the 216 possible two-step behavioral transitions. Transitions from four of the six possible starting behaviors occurred frequently enough to permit this extensive analysis (F, OH, AL, and RST). The expected and observed probabilities were placed in 6×6 matrices for comparison. The matrices for starting behavior a = AL from data set 2 are tabulated and plotted in Figure 5. The expected and observed three-dimensional plots of behavioral frequency show peaks and valleys at the same positions and with approximately the same amplitudes.

We attempted to test the significance of differences between the expected and observed 6×6 matrices by calculating chi-square values. When the two data sets were treated separately, chi-square scores ranged from 42.5, for set 2, starting behavior AL, to 62.9 for set 1, starting behavior F. When both sets of data were pooled, chi-square scores ranged from 66.5 to 81.5. All the chi-square values were significant by standard tests using 25 degrees of freedom ($P < 0.001$ to $P < 0.01$). The chi-square statistic is known to be unreliable, however, in the case of behavior-sequence matrices with cells containing low values (Chatfield and Lemon, 1970), and the two-step transition matrices we tabulated have a number of cells with values of 0. Also, variation in transition rates was high among individuals (CV for $F \rightarrow F$ as high as 157%), which adds to the chi-square score. The presence of this type of added uncertainty is demonstrated by the fact that higher scores result when data from two periods of observation are pooled. Instead of a chi-square test, Chatfield and Lemon (1970) suggest selecting the most frequent sequences and comparing expected and observed values by inspection. The plots of Figure 5 follow that principle and show that the two-step transition predictions match the observations fairly well.

Behavioral dwell-time distributions

We defined behavioral dwell time as the duration of a continuous single bout of the same behavior. This is

equivalent to the 'interval distribution' (Heiligenberg, 1973) or the 'hazard function' (Cox and Lewis, 1966) but differs in that exits into any other behavioral state are allowed. Dwell-time histograms for four of the six behaviors are plotted in Figure 6. If behavioral choice is determined stochastically, the distribution of dwell times will be exponential. R/OH and R/AL behaviors did not occur frequently enough to permit dwell-time analysis. OH and AL dwell times were exponentially distributed. F dwell times were also exponentially distributed, with the exception of a few lengthy episodes. The presence of longer episodes has implications for the organization of the feeding neural network and suggests that the network may be modulated by stimuli such as the presence of stray food organisms or by a long-lasting effect of food presented on the previous day (Watson and Chester, 1993). The RST dwell-time histogram was best fit by the sum of two exponentials. This suggests two possibilities: first, there may be two resting states which have independent transition probabilities but are indistinguishable by observation; alternatively, the transition probabilities for exiting RST may vary with time spent in the RST behavior.

Discussion

These observations demonstrate that spontaneously evolving sequences of behavioral transitions in *Melibe leonina* are stochastic such that the probability of a given transition is independent of preceding ones. At the same time, behavior is organized by the fact that transitions between behaviors within a mode are more likely than transitions between behaviors in different modes. This creates a *cul-de-sac* within the transition-probability matrix so that one behavior pattern can only be reached by way of another. As a result, the organization is not inconsistent with hierarchical models of behavioral organization like that proposed by Tinbergen (1951) since specific stimuli might move the animal into a mode in which certain behaviors are more likely than others even though the individual transition probabilities are constant and independent. This view is supported by evidence that the neural circuits underlying spontaneous behavioral choice are influenced by external cues such as the presence of prey and by physiological signals correlated with body size.

Spontaneous behavior in *Melibe* demonstrates two features characteristic of a stochastic system. First, the two-step transition probabilities predicted from consideration of measured single-step transition frequencies closely match the two-step frequencies observed experimentally. This shows that behavioral transitions are influenced by the starting behavior but not by previous behaviors. Second, for three of the four behaviors for which

		EXPECTED								OBSERVED					
		c								c					
a=AL	b	F	OH	AL	R/OH	R/AL	RST	a=AL	b	F	OH	AL	R/OH	R/AL	RST
	F	8.8	4.1	2.1	2.6	1.5	0.3		F	5	4	6	0	4	1
	OH	5.3	10.3	7.3	2.3	1.2	1.2		OH	5	7	9	5	0	2
	AL	10.0	14.4	81.2	6.2	15.5	27		AL	10	12	96	3	12	27
	R/OH	3.2	2.3	1.2	2.6	1.5	0.9		R/OH	1	2	2	4	2	1
	R/AL	4.1	3.5	13.2	4.1	3.5	1.2		R/AL	3	2	14	3	5	1
	RST	0.3	1.2	13.2	0.6	2.6	33.7		RST	0	0	11	2	5	27

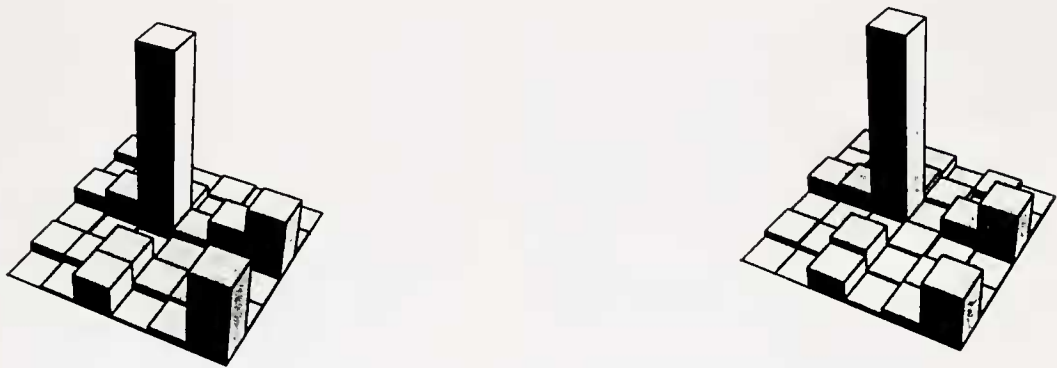


Figure 5. Top. Expected and observed two-step transitions with data from starting behavior AL (set 2). Expected numbers were calculated from single-step transition frequencies using the equation $P(a \rightarrow b \rightarrow c) = P(a)P(a \rightarrow b)P(b \rightarrow c)$ (see text). Bottom. 3-D plots corresponding to the expected and observed two-step transition matrices.

there was sufficient data to evaluate behavioral dwell-time distributions, dwell times were distributed exponentially. This supports a model based on independent and unvarying transition probabilities. The dwell-time distribution for the exception, the RST behavior, was best fit by the sum of two exponentials. This result might be explained by the existence of two resting states with different average duration. We were unable to identify multiple resting states but, like sleep and quiescent behavior in other animals, the two states may have a different neurophysiological basis while appearing identical to the observer. Another possible interpretation is that the exit probability from RST decreases with time spent in the RST state, perhaps reflecting a decrease in arousal. The data are not sufficient to evaluate these possibilities, but they raise questions of a general nature that might be accessible to neurophysiological investigation in *Melibe*.

A property that emerges from a consideration of the transition-probability matrix is that spontaneous behavior can be interpreted as a series of jumps between two

modes named the *feeding mode* and the *resting mode*. This grouping of behaviors follows directly from the one-step transition probabilities and the observation that transits within modes are far more probable than transits between modes. It is a robust conclusion based on over 1900 observations of transitions, far more than the 360 ($10 n^2$) required to analyze a repertoire of n behaviors (Fagen and Young, 1978). This organization represents a way in which higher order structure can be generated by a coupled system of first-order random processes.

The probability of transitions between modes did not fluctuate during 6 h observations, but this period is short relative to the life span of the animal. Preliminary data suggest that transition frequencies do change with maturation and that juveniles demonstrate both a different repertoire of behaviors and different frequencies of transitions between the behaviors they share with adults (S.E. Gelber, pers. comm.). In addition, Watson and Trimarchi (1992) have shown that the presence of prey organisms, sensed in response to chemical and tactile cues (Watson and Chester, 1993), influences feeding dwell

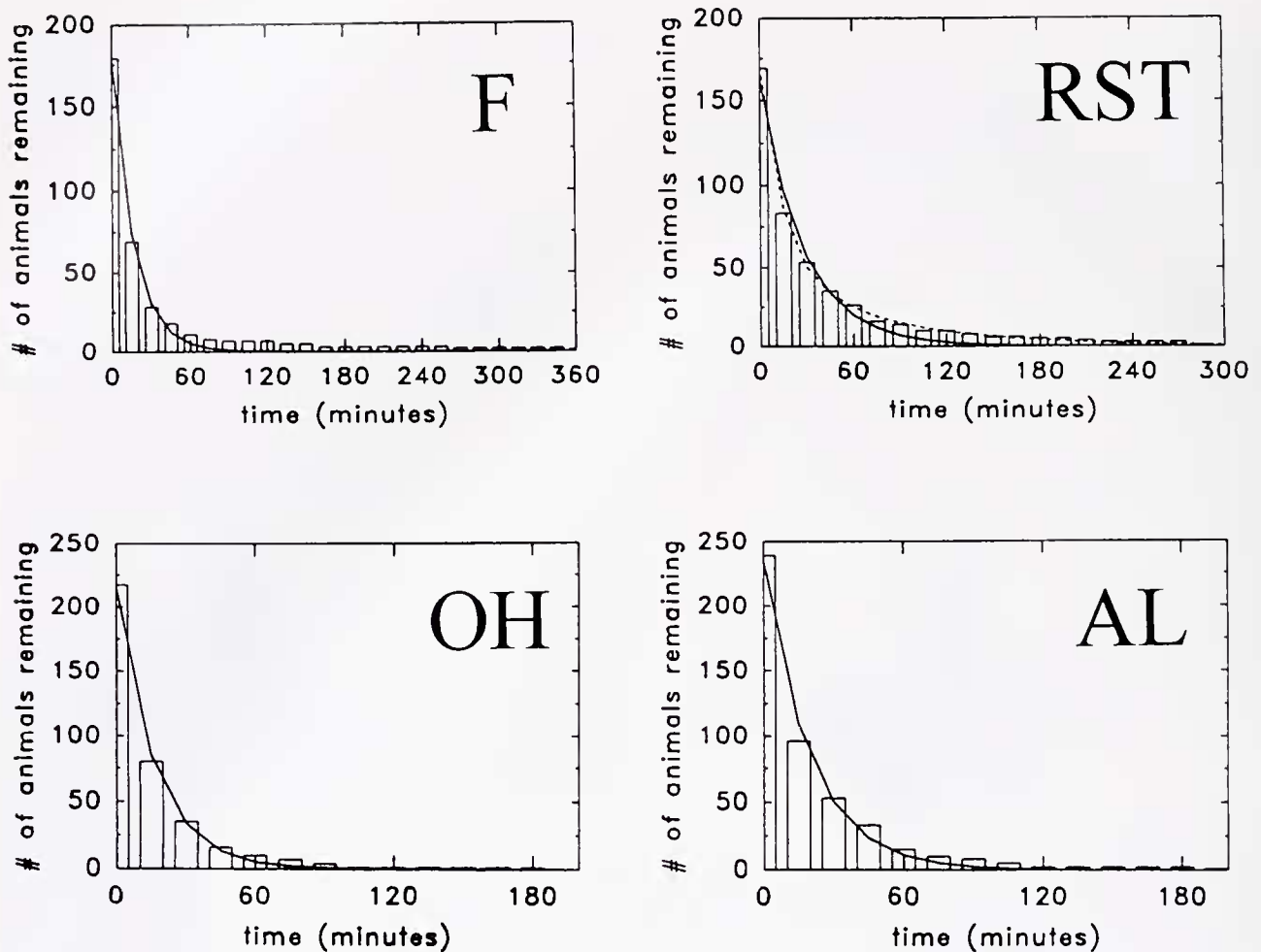


Figure 6. Dwell-time histograms for feeding (F), open hood (OH), resting (RST), and alert-processes extended (AL) behaviors. The OH and AL distributions are fit by exponentials (solid curve), consistent with the exit from these behaviors being random. The feeding (F) dwell-time distribution is also approximately exponential, except for outlying points that account for 1% of the data. The outlying points with long dwell times may reflect behavior driven by external stimulation. Two fits are plotted for the resting (RST) data, a single exponential (solid line) and the sum of two exponentials (dashed line). All distributions were fitted using a nonlinear least-squares method.

time in a fashion that is graded with the concentration of prey.

A particular pair of behavioral transitions, OH \leftrightarrow AL, acts as a gateway between the feeding and resting behavior modes. The OH and AL behaviors share features of body posture such as the positions of the rhinophores and cerata, but they differ in oral hood posture. The change between behavior modes, therefore, is bridged by a relatively small postural adjustment, but it signals a long-term change in the animal's behavior pattern. A neurophysiological interpretation is that slight but measurable shifts in the activities of neurons involved in OH and AL behaviors can result in a stable, lasting shift in motor-system function.

Increased body size is correlated with an increase in

time spent feeding, but the average dwell time of feeding episodes is independent of size. This suggests that the probability of entering feeding behavior increases with body size. Conversely, it is apparent that the presence of food organisms decreases the probability of exit from feeding but does not have a clear effect on entry into feeding behavior. If we assume that separate entry and exit circuits govern transitions into and out of the feeding state, it should be possible to measure changes in excitability in those circuits that correspond to the behavioral observations. One simple and testable prediction is that body size modulates the entry circuit, while the presence of food modulates the exit circuit. Modulation of the exit circuit by food could confer competitive advantage by maximizing foraging efficiency in the face of a variable

food supply. Such shifts in behavioral transition probabilities might be mediated by neuromodulatory or hormonal effects that cause a dynamic restructuring of neural networks by influencing either postsynaptic excitability or the amplitudes of synaptic potentials (Gettings, 1989; Katz *et al.*, 1994).

Neuronal circuits that mediate behavior in *Melibe* can be studied with intracellular recording in a whole-animal preparation using techniques pioneered by Willows (1973) and Gettings (1981). Using this preparation, we have made progress in elucidating the networks involved in swimming locomotion and feeding movements of the oral hood; Cohen *et al.* (1991) have succeeded in using optical imaging techniques to monitor activity simultaneously in dozens of neurons in the *Melibe* buccal ganglion. Neurophysiological methods are available, therefore, to study changes in neuronal function that are correlated with behavioral choice. The behavioral model developed here provides a framework for the interpretation of physiological experiments.

Acknowledgments

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